Hurricane Impact on Uplands and Freshwater Swamp Forest

Large trees and epiphytes sustained the greatest damage during Hurricane Andrew

Lloyd Loope, Michael Duever, Alan Herndon, James Snyder, and Deborah Jansen

The path of Hurricane Andrew, one of the strongest hurricanes in US history, by chance touched on the core of a complex mosaic of terrestrial vegetation comprised of an assemblage of plant species markedly different from that found anywhere else in the continental United States. The three southern counties of Florida—Dade, Monroe, and Collier—lie south of 25°N and possess a flora in which more than 60% of the vascular plant species are of West Indian origin (Long 1974). Of the 130 tree species native to South Florida, 112 have an otherwise tropical distribution; in Florida, they are at the northern limit of their distributions (Tomlinson 1980).

A majority of the West Indian plant species occur in forest ecosystems growing on limestone substrates, most notably in pine forests and tropical hardwood forests or hammocks, elevated slightly (generally 0–2 m) above surrounding marshlands, so that flooding is only occasional. These upland sites cover only approximately 4% of Everglades National Park (Olmsted and Loope 1984), a similarly small percentage of southern Big Cypress National Preserve, and perhaps 50% of the land portion of Biscayne National Park. By chance, a remarkably high percentage of the forest stands with West Indian flora were within the narrow path of Hurricane Andrew.

It is difficult to predict how the opening of the canopy will affect animals and understory plants

This article is a preliminary evaluation of the hurricane's effects on vegetation and on selected plant and animal species of upland forests (pinelands and hammocks) and associated freshwater swamp forests (cypress forests and bayheads). It also addresses the posthurricane spread of invasive exotic plant species. It is based on nine days of observations from helicopter and the ground during 13–21 September 1992, combined with our past field experience and that of colleagues in ecosystems of southern Florida.

Hardwood and pine forest canopies and epiphytic vascular plant populations were modified dramatically. Immediate changes to understory plant species and vertebrate animal populations were generally more subtle.

Lloyd Loope is a research scientist at Haleakala National Park, Makawao Maui, HI 96768. Michael Duever is an ecologist at the National Audubon Society, Naples, FL 33964. Alan Herndon is a graduate student in the Department of Biological Sciences, Florida International University, Miami, FL 33199. James Snyder is a research biologist and Deborah Jansen is a wildlife biologist at Big Cypress National Preserve, Ochopee, FL 33943.

Effects on vegetation

Damage to woody vegetation was most severe in or near the eye of Hurricane Andrew. As one moved away from the storm track, fewer and fewer individual trees or patches of forest showed evidence of major damage, and they increasingly exhibited only loss of branches instead of stem breakage or uprooting. There was a virtually complete loss of leaves from hardwood trees along the central track of the storm, grading to only a general thinning of leaves near the margins of the storm-affected area. Defoliation and loss of small branches affect community productivity in the short term, but recovery to predisturbance conditions should occur rapidly from these types of impacts. Major structural damage—loss of entire larger branches, bent stems, main stem breakage, and uprooting—result in longer-term effects on the community as well as on the trees themselves.

Pineland. The Long Pine Key area,[1] the largest upland area of Everglades National Park (approximately 8000 ha), is occupied by a mosaic of pineland and tropical hardwood vegetation on a rough limestone (Miami oolite) substrate with abundant crevices and solution holes and little soil development. South Florida slash pine (*Pinus elliottii* var. *densa*) forms an open canopy with much

[1]Place names are given on the map on page 228.

light reaching the forest floor. The understory is diverse, with approximately 50 woody species, primarily of West Indian origin, and more than 120 forbs and graminoids, including approximately 20 taxa endemic to South Florida (Olmsted et al. 1983, Snyder et al. 1990). Similar pine forests, confined to Dade County, once covered approximately 74,000 ha, extending northeastward along the Miami Rock Ridge to North Miami, but outside the park the farming and urban expansion have almost completely replaced them (Snyder et al. 1990).

Robertson (1953) argued that the large number of light-requiring endemic species strongly suggests a history of fire in the pinelands. Primarily based on Robertson's work, Everglades pinelands have been intensively managed for almost 30 years, using prescribed fire at intervals of 3–7 years (Everglades National Park 1991). This fire regime maintains a diverse understory, preventing shading out of the numerous herbaceous species that resprout from underground parts after fire. Almost all species of the pine forest, both herbaceous and woody, normally survive fire by resprouting. The mature pines present regenerated around 1940 after logging operations stopped there, just before the establishment of the park. Prescribed fires have only rarely killed them. By 1992, the pines had attained heights of 15–20 m and diameters of 20–30 cm.

Hurricane Andrew radically changed the structure of Long Pine Key pinelands. Based on data gathered by the park Fire Management Program, the pre-Andrew pine forest contained an average of 318 mature trees/ha. (Trees were defined as mature when they have diameters of more than 17.8 cm). Of these, approximately 100/ha were downed by the hurricane. The pines snapped at heights of 1–6 m; approximately 2–3 times as many pines had snapped boles as were uprooted. Pines forming the surviving canopy lost some needles, but they retained a substantial amount of live foliage after the storm. The removal of one-third of the pines created canopy openings and is expected to allow recruitment of pine saplings into the overstory.

Wind-snapped pine trees in forest of Long Pine Key. Photo: James Snyder.

Seedlings and saplings grow more rapidly with increased availability of light and nutrients. Fires are expected to be cooler for a period because of lessened needle accumulation in the canopy gaps, thus more young trees can survive.

We observed the pineland understory to be relatively unaffected by Andrew. The pines apparently broke the force of the wind, and little damage occurred to leaves of understory shrubs and herbs. On understory hardwoods (heights less than or equal to 3 m), leaf damage, minor stem breakage, and some bark damage comprised the maximal effect observed.

The Fire Management Program (Everglades National Park 1992) concluded that, although increased fuels are present, no substantive change in the fire program is needed. The quantity of added fine fuels (needles and twigs) is small in relation to the fine fuels normally present. Increased coarse fuels (branches and trunks), however, are predicted to increase two- to fourfold the smoke generated; the air quality effects are not entirely clear. The program also predicted that, after approximately two years, the holes in the canopy of the Long Pine Key hammocks would be patched by vines and fast-growing tree species (i.e., *Trema*), creating an envelope reducing moisture loss. Although the new closed canopy would have little resemblance to a mature canopy, the hammocks would regain normal soil-moisture retention.

The extensive pine forests of Big Cypress National Preserve are also made up of South Florida slash pine but occur on shallow sandy soils overlying a limestone formation (Tamiami Limestone) having fewer larger solution holes than does the Miami Rock Ridge pinelands. Most of the Big Cypress forests were on the north side of Andrew's path. However, an area in southern Big Cypress known as Lostmans Pines, with several unlogged, old-growth pine stands, suffered substantial damage (broken boles, uprooting) among large trees; 41% of trees larger than 25 cm in diameter were downed.

Tropical hardwood hammocks. Tropical broad-leaved forest occurs in peninsular South Florida in hammocks (Snyder et al. 1990 describe them in detail). Our use of the term *hammocks* refers to forest vegetation comprised of flood-intolerant, West Indian tree species. Hammocks generally occur on a limestone rockland substrate and less commonly on a sandy or marl substrate; those affected by Hurricane Andrew are primarily on rockland, with tree roots firmly intertwined in the channels and fissures in the limestone as well as in the shallow veneer of organic soil, resulting in strong an-

Trees of buttonwood (*Conocarpus erectus*) on the eastern shore of Elliott Key in Biscayne National Park took a fierce beating from the winds and storm surge of Hurricane Andrew, yet most narrowly survived and have since regenerated branches and leaves. Photo: L. Loope, September 1992.

choring. Where interspersed within a matrix of pineland, hammocks occur on higher sites with subtle differences in the limestone bedrock (Craighead 1971). Hammocks of the islands in Biscayne National Park occur on the Key Largo Limestone with varying amounts of accumulated organic soil.

Andrew's effects on the forests of Elliott Key in Biscayne National Park were dramatic. Where large trees occurred in the hammock forest, they were extensively damaged (20–30% downed, and large branches sheared off almost all the trees). Stands of shorter, smaller-diameter trees survived with much less damage, often with loss of only minor branches. Defoliation was virtually complete, even near ground level. Leaf and other natural litter was removed within 100–200 m of the shore in areas hit by a high storm surge. A heavy deposit of litter and debris often marked the inland limit of the storm surge. Storm surge affected both sides of Elliott Key, but appeared to have been stronger on the side of the island facing the mainland. Erosion due to the storm surge was found to be minimal.

The hurricane's effects on island hammock forests diminished southward from its eye. From the air, old-growth forests on Old Rhodes and Totten Key appeared largely spared of major damage. The hammock forest on south Totten Key comprises perhaps the best remaining example of old-growth forest in the Florida Keys.[2] This forest is particularly notable for large-diameter trees and, in particular, for its many large individuals of lignum vitae (*Guaiacum sanctum*, Zygophyllaceae). Some of these trees have been repeatedly windthrown by hurricanes but resprouted.

Mahogany Hammock, one of the hammocks best-known to Everglades National Park visitors because its boardwalk trail makes access easy, was on the fringes of the most severe part of the storm. As a result, it was less damaged by Andrew than by Hurricane Donna in 1960 (see page 261), based on the account and photos of Craighead and Gilbert (1962). It was also much less affected by Andrew than were the Long Pine Key hammocks, approximately 15–20 km to the northeast. Still, many large branches of mahogany (*Swietenia mahagoni*) were broken, but few trees were uprooted (approximately 1% of all the trees more than 10 cm in diameter).

Hurricane Andrew's effects were as spectacular in Long Pine Key hammocks and Shark River Slough as anywhere in the natural vegetation of South Florida. We estimated that in Long Pine Key at least 20–30% of trees more than 10 cm in diameter were uprooted or had their main stems broken. Almost all trees lost large and small branches. Canopy cover was reduced from nearly 100% cover to approximately 30%, and canopy gaps on the order of 10–20 m wide are now common. The abundance of fallen trees and large limbs made our movement through the hammocks extremely difficult.

Hammock trees are shorter than are pines, but they are more susceptible to wind damage. (Heights are

[2]W. B. Robertson, 1992, personal communication. South Florida Research Center, Everglades National Park, Homestead, FL.

typically less than 14–16 m for wild tamarind, *Lysiloma latisiliqua*; live oak, *Quercus virginiana*; willow bustic, *Bumelia salicifolia*; and gumbo limbo, *Bursera simaruba*, trees.) Tall, large-diameter trees seemed most susceptible to hurricane damage of all types. Andrew hit live oaks particularly hard. Large ones, 15 m tall and 75 cm in diameter, typically lost many branches, including ones as large as 45 cm in diameter. Shorter trees were frequently knocked over or broken by the falling of larger trees, but they rarely showed major wind damage. Virtually all the trees of Long Pine Key hammocks were completely defoliated except the oaks, which were only partly defoliated. However, their leathery leaves were battered. For most hammock species, releafing was well advanced 3–4 weeks after the hurricane. Oaks were slower at releafing than other species; gumbo limbo and wild tamarind were faster.

In hammocks not affected by the coastal storm surge, understory plants less than 2 m tall and seedlings and saplings of the overstory trees appear to have fared well during the storm. Most of these plants retained at least part of their foliage after the hurricane.

In Long Pine Key hammocks, vines started rapid growth in response to canopy opening within a month after the storm. Typical were grapevines (*Vitis* spp.), poison ivy (*Toxicodendron radicans*), and Virginia creeper (*Parthenocissus quinquefolia*). They are expected to conserve soil moisture but also prevent establishment of tree seedlings and possibly smother some of the partially uprooted trees.

Hammocks in the extreme southern portion of Big Cypress National Preserve were also strongly affected by the hurricane. Farther north the damage was more localized and less severe.

Whigham et al. (1991) discuss hurricane impacts to a dry tropical forest in the northeastern Yucatan Peninsula, a habitat that resembles the hammocks of South Florida. Hurricane Gilbert had winds of 300 km/hr. Effects were roughly similar to those observed in Long Pine Key hammocks and locally on Elliott Key after Andrew. All trees were damaged and defoliated by Hurricane Gilbert, and most had only their largest branches remaining. After two years, 12% of the 1447 trees in their plots had died, including only 16% of those uprooted and 29% of those with snapped trunks. The authors suggest that low rates of tree mortality indicate that forest composition may change little as a result of the hurricane. Whigham et al. (1991) stated that "most species at our site resprouted within one month, and the canopies of most trees had recovered dramatically within one year." Frangi and Lugo (1991), Walker (1991), Yih et al. (1991), and Duever and McCollom (1992) examining effects of other hurricanes reported similar findings and expected little change in species composition.

Fires after Hurricane Gilbert had a greater impact on tree mortality than did the hurricane itself on forests of the northeastern Yucatan, where mean annual precipitation is approximately 1100 mm (versus, in Florida, 1161 mm at Flamingo and 1600 mm at Homestead). Craighead and Gilbert (1962) stated that severe fires followed the 1935 hurricane in South Florida, with losses particularly severe to mahoganies between Crocodile Point and Flamingo.

Loss of major limbs, broken trunks, and uprooting from Hurricane Andrew are expected to produce lasting changes, because many years of growth will be necessary to reconstruct lost canopy. During at least the early portion of that period, we predict the microclimate of hammocks will be very different from pre-hurricane conditions. Hammock soils will dry out faster due to increased sunlight and decreased relative humidity in hammocks. Because fire managers at Everglades National Park plan to continue to use hammock soil moisture as an index of whether or not burning in pinelands is safe, there will be less prescriptive burning. Forest managers at Big Cypress plan to take a similar approach. The greatest fire hazard of all may be on the islands at Biscayne, where generally drier conditions prevail; an ignition could cause a conflagration during a prolonged drought.

Bayheads. Mature bayheads are closed-canopy forests on peat substrate consisting of tree species adapted to prolonged flooding (ground surface inundated 2–6 months each year). Maximal canopy height is 8–10 m. Red bay (*Persea borbonia*), sweet bay (*Magnolia virginiana*), dahoon holly (*Ilex cassine*), willow (*Salix caroliniana*), wax myrtle (*Myrica cerifera*), and cocoplum (*Chrysobalanus icaco*) make up these stands. Pondapple (*Annona glabra*) often grows at the forest margin. The canopy of a mature bayhead is often so dense that the shaded understory is composed only of scattered individuals of swamp fern (*Blechnum serrulatum*) and leather fern (*Acrostichum danaefolium*).

Bayhead swamp forests resemble bayheads in most characteristics except that the canopy is open with a luxuriant understory (with, for example, sawgrass, *Cladium jamaicense*; buttonbush, *Cephalanthus occidentalis*; and cattail, *Typha latifolia*). The forests typically occur in Shark River Slough as the downstream portion of tree islands that have at the upstream end a hardwood hammock on a bedrock platform.

Hurricane Andrew had strong, but variable, immediate effects on the structure of bayhead vegetation. The wind broke few tree trunks, although it often snapped large branches. Uprooted trees were common, but scattered in occurrence, except in the case of wax myrtle, which was uprooted consistently. Many bayhead trees were left standing, even in Shark River Slough. There was notably less damage to the woody canopy structure in bayheads than in adjoining hammocks at Panther Mound and other Shark River Slough hammocks. Willows were notably unaffected by the hurricane; it completely defoliated shrubs, but releafing was well under way within three weeks.

Cypress forests. Cypress-dominated forests (*Taxodium distichum*) are the most widespread vegetation type in Big Cypress National Preserve, but they are a minor component in Everglades National Park. They occur low along the water-level gradi-

ent, and variations in forest structure and composition reflect their position along this gradient (Duever et al. 1984). Cypress trees toward the deeper centers of topographic depressions are older or they may grow more rapidly, resulting in progressively taller trees toward the center. Thus, the domed cross-sectional shape results in the stands of trees over round depressions being called *domes* and those over linear depressions being called *strands* (Duever et al. 1984). Major variations in this forest type include mixed swamp forests, cypress forests, and dwarf or scrub cypress savannas.

In general, cypress showed modest hurricane effects over the area of the storm's influence, although in scattered sites numerous trees suffered major damage. Even in the most heavily affected areas, cypress trees retained some of their leaves. In less affected areas, there was only thinning of the leaves, which had begun to show their fall colors before the hurricane. September is well past the growing season of cypress, but some of the trees were releafing after the hurricane. Because the vast majority of the trees retained even small branches, releafing should approximate normal during the coming growing season.

In the vicinity of the hurricane eye, 1–2% of the cypress suffered major damage, that is, broken stems or uprooting. Moving out from the eye, significant damage became much less frequent, being confined primarily to scattered individuals or patches of forest. This pattern held for dwarf cypress as well as for the larger cypress trees in the dense domes and strands.

Cypress appeared to suffer much less damage from Hurricane Andrew than it did in South Carolina from Hurricane Hugo in 1989.[3] A total of 46% of the cypress in South Carolina sustained major damage, whereas in South Florida, the storm's major damage affected less than 5% of the trees. The smaller size of cypress trees in South Florida areas affected by Hurricane Andrew may be the primary reason for this difference. Other evidence that larger trees are likely more vulnerable to major damage comes from Corkscrew Swamp in southwest Florida. There, almost all old-growth (more than 300 years old) cypress have lost upper portions of stems or major branches, probably as a result of past hurricanes (Duever et al. 1984). Staff at Corkscrew Swamp Sanctuary estimated that Hurricane Donna in 1960 (see page 261) caused major damage to approximately 30% of the large cypress trees.

[3]M. Duever, 1992, personal observations.

Hurricane effects on rare plants

The South Florida national parks affected by Hurricane Andrew comprise a major refuge for rare and localized plant species. Loope and Avery (1979) predicted which species were likely to be threatened by hurricanes. With limited time and lack of quantitative baseline data, we have only been able to make educated guesses of the impact of Hurricane Andrew. The greatest mortality was observed among epiphytes.

Endemics. At least 27 endemic plant taxa occur in National Park Service areas of southern Florida, primarily in the rockland pine forests (Avery and Loope 1980). Most are herbaceous plants, but three are shrubs or small trees. In general, the winds did not noticeably affect herb and shrub layers in the pinelands. We saw no notable wind damage to understory vegetation in any site, so the endemics are not likely to have suffered significant damage. Tree falls are the most significant source of direct hurricane damage, and they affected less than 5% of the ground surface.

West Indian species. Many West Indian plant species reach their northern limits in southern Florida, where many of these species are uncommon. We subdivide the uncommon West Indian species into five groups: terrestrial ferns, terrestrial orchids, palms, tropical hardwoods, and epiphytes.

Tropical terrestrial ferns most vulnerable to effects of Hurricane Andrew are *Adiantum melanoleucum*, *Lomariopsis kunzeana*, and *Sphenomeris clavata*. The first two are known from limestone-solution holes in a single hammock in Long Pine Key of Everglades National Park. None of the three species was seen during our brief survey. However, based on observations of more common ferns in similar habitats, they probably survived.

Vulnerable terrestrial orchids in the storm-affected area are *Centrogenium setaceum*, *Galeandra beyrichii*, *Erythrodes querceticola*, *Spiranthes costaricensis*, and *Spiranthes cranicoides*. It is possible only to study these orchids for a brief portion of the year because plants are totally underground except during the month or two when a species blooms. For this reason, we predict they suffered little direct damage. *Centrogenium* and *Spiranthes costaricensis* have rapidly expanded their ranges in the past decade,[4] perhaps prefering denser shade. If so, the thinning of hammock canopies will harm their populations.

Four species of uncommon or rare palms occur in park areas that Hurricane Andrew affected. These are silver thatch palm (*Coccothrinax argentata*), buccaneer palm (*Pseudophoenix sargentii*), royal palm (*Roystonea elata*), and Florida thatch palm (*Thrinax radiata*). All except buccaneer palm have substantial wild populations outside the area of major hurricane damage. In general, palms are well adapted structurally to hurricanes, and they survived with less apparent damage than any other group of plants.

Buccaneer palm is endangered in Florida, although it is not uncommon in the Caribbean and Mexico. A population of 13 wild individuals was known on Elliott Key before Hurricane Andrew. We were unable to visit this population, but on 19 September we were shown two groups of three seedlings planted on Elliott Key two years ago, in cooperation with Fairchild Tropical Garden and the Center for Plant Conservation. Four of the six seedlings, each approximately 1 m tall, had survived with no damage; one was uprooted and dead; we could not find the sixth. The now-open canopy in the hammock may allow the sur-

[4]C. McCartney, 1992, personal communication. Hollywood, FL.

viving seedlings to grow rapidly in the near future, so that the net effect of the hurricane on this species may be beneficial.

Tropical hardwoods of concern in the affected areas are *Colubrina arborescens*, *Eupatorium villosum*, *Ilex krugiana*, *Guaiacum sanctum*, *Hypelate trifoliata*, and *Jacquinea keyensis*. The latter three species also have substantial populations outside the affected areas. *Colubrina*, *Eupatorium*, *Hypelate*, *Ilex*, and *Jacquinea* are shrubs or small trees in the shrub layer of Long Pine Key pinelands. The storm caused little direct damage to this layer.

Vascular epiphytes are overwhelmingly tropical in distribution, and 29 species reach their northern limits in southern Florida. Our observations suggested that epiphytes suffered more mortality from the storm than any other plants as a result of their growth in locations particularly susceptible to wind damage (i.e., tree branches and trunks). The storm destroyed approximately 90% of canopy epiphyte individuals. Our general impression was that a sufficient number of individuals of common epiphytes in hammocks survived to ensure recovery. Many *Tillandsia* plants in the subcanopy were badly sunburned due to the loss of canopy shade, but we found many healthy individuals in more-protected locations. Epiphytic orchids appear to be less susceptible to sudden increases in light level than bromeliads. Protected sites will increase with the active releafing of defoliated canopy trees. Approximately 50% of the subcanopy epiphytes were lost. Epiphytes are also expected to be more susceptible to freezes and droughts for the next several years due to the reduced canopy.

Canopy thinning by the hurricane may strongly promote the growth and spread of populations of canopy epiphytes in Long Pine Key. The canopy epiphytes of most concern, *Catopsis berteroniana*, *Catopsis floribunda*, *Tillandsia flexuosa*, and *Tillandsia pruinosa*, occur widely in protected areas of southern Florida, and, although the loss of some local populations in the Long Pine Key and Ten Thousand Islands area is likely, survival of the epiphyte species in Florida is not jeopardized.

Hurricane effects on wildlife

Based on available evidence, few wildlife species were negatively affected by Hurricane Andrew. However, there is special concern about the fates of the red-cockaded woodpecker, several species of tree snail, and a rare butterfly.

Red-cockaded woodpecker. The red-cockaded woodpecker (*Picoides borealis*), a federally endangered species, is endemic to coastal plain pinelands of the southeastern United States. It excavates its nesting and roosting cavities in living pine trees (Walters 1991). The woodpeckers require old-growth trees infected with the fungus *Phellus (Fomes)pini*, which softens the heartwood. Birds of the species form groups consisting of a mated pair with two to five unmated birds acting as helpers during the nesting cycle. Roosting and nesting occurs in the same cluster of trees year after year. This woodpecker formerly occupied pinelands of the Miami rock ridge (including those of Everglades National Park), but disappeared from that part of its range during the 1960s (Snyder et al. 1990). Populations survive in Big Cypress Swamp (Patterson and Robertson 1981).

Hurricane Andrew damaged an area of old-growth pines (Lostmans Pines) in the extreme southwestern corner of Big Cypress National Preserve. Eight clusters of woodpeckers have been monitored there since the early 1980s, and the population is apparently declining. During the summer of 1991, a total of five birds (two pairs and one single male) were seen in three clusters. In 1992, these five birds were still alive but attempted nesting at only one site. We could find only a single male after the hurricane. In the three active clusters, we located 33 of 36 known cavity trees. Of the 33, 2 (6%) were uprooted, 15 (45%) were snapped at the cavity, 12 (36%) had trunks broken at locations other than at the cavity, and 4 (12%) were intact.

Florida panther. The Florida panther (*Felis concolor coryi*) is federally endangered; panthers probably survive in the eastern United States only in Florida. Within Everglades National Park, studies document the gradual disappearance of the species. In August, four radiocollared panthers occupied parklands south of Interstate 75 (Alligator Alley, a road north of Tamiani Trail). All were there on Saturday, 22 August, before the hurricane and on Tuesday, 25 August, the day after the hurricane. Three of the four panthers were north of US Highway 41 (Tamiami Trail) in Big Cypress, in habitat only slightly affected by Andrew. The fourth panther was present on both days in a group of hammocks approximately 1.5 km south of US Highway 41. There was moderate damage, in the form of patches of downed hardwood trees, but these did not affect the panther's normal movement pattern.[5]

White-tailed deer. White-tailed deer (*Odocoileus virginianus*) receive special attention in South Florida parks because of their importance as the primary prey of the Florida panther and because they are intensively hunted by sport hunters within most of Big Cypress. Before the hurricane, 32 radiotransmitting deer had been monitored once a month.[6] All of these deer survived the hurricane. Although the hurricane locally diminished the deer forage and cover, we expect both to recover rapidly.

American swallow-tailed kite. Pine forests of Long Pine Key comprise an important breeding and premigration staging area for the small remaining US population of American swallow-tailed kites (*Elanoides forficatus*). The tallest pine trees are used for nesting; 15–20 territories are active annually.[7] Because the kites had already migrated south before the storm, there was no direct impact, but the loss of nesting trees may affect the kites' future nesting success.

[5]D. Jansen, 1992, personal observations.
[6]R. F. Labisky, 1992, personal communication. University of Florida, Gainesville.
[7]K. D. Meyer, 1992, personal communication. Big Cypress National Preserve, Naples, FL.

Elongated tree islands, scattered throughout the marshes of Shark River Slough, are shown in their pre-Andrew condition, with domelike hardwood forest on the upstream (right) ends and bayhead swamp forest downstream. Photo: Stuart Pimm, May 1992.

Hurricane Andrew left few trees standing in this Shark River Slough tree island. Photo: Stuart Pimm, September 1992.

South Florida tree snail. The South Florida tree snail, *Liguus fasciatus*, is endemic to Florida's Dade, Broward, Monroe, and Collier counties (where they inhabit tropical hardwood hammocks); Cuba; and the Isle of Pines. Eight subspecies and numerous color forms have been recognized. Many color forms are highly localized; some have been extirpated (Deisler 1982). Due to the diverse color patterns on the shells, these snails attract much attention.

Based on a visit to a hammock near Cutler Ridge five days after Andrew, Emmel (1992) reported that *Liguus* and other tree snails were faring poorly under a completely defoliated canopy. During our survey two to three weeks later, releafing was well advanced providing partial canopy recovery. We frequently saw apparently thriving *Liguus* in numerous hammocks in the Everglades and Big Cypress; they were more conspicuous than usual due to the reduced foliage in the hammocks. We saw no *Liguus* in our survey of Elliott Key, but populations there have been very small or absent in recent years (Deisler 1982) in any case. In the hammocks of Everglades, we saw no signs of recent mortality. However, in several Big Cypress hammocks, recently dead snails were found on the ground or floating in the water.

Future effects on the snails are difficult to predict. Increased light may increase the food supply for *Liguus*, leading to a long-term population increase. *Liguus* feeds primarily on epiphytic algae and fungi and is usually most common in the areas of the hammocks with thinner canopies.[8] However, the sparsity of cover over the next few years will leave the snails more susceptible to freezes, drought, and fire and may allow predators to find them more easily.

Butterflies. Adult butterflies were much less common than normal in southern Florida during our surveys. Even in areas little affected by the hurricane, we saw adults infrequently, and they appeared to be newly emerged. Because plants were just beginning to flower post-hurricane in mid-September, it is likely that adults surviving the storm itself died before food resources became available. Long-term effects of a major hurricane could be substantial.

Schaus' swallowtail (*Heraclides aristodemus ponceanus*) is a federally listed endangered subspecies, endemic to southeastern Florida and now restricted to localized colonies on Elliott Key and north Key Largo. Andrew severely affected its known habitat in hammocks of Elliott Key, in the Petrel Point area. The adult flight period is from late April to early June. Females deposit eggs on the undersides of leaves of the larval food plants of torchwood (*Amyris elemifera*) and wild lime (*Zanthoxylum fagara*; Baggett 1982). Researchers from University of Florida[9] counted the Petrel Point population in May 1992. Our observations suggest that Andrew completely defoliated both host plant species in this area, and it is likely that this Schaus' swallowtail population has been severely depleted.

Exotic plants

The paperbark tree *Melaleuca quinquenervia* (Myrtaceae) is the most invasive plant species in South Florida (Hofstetter 1991) and in Big Cypress National Preserve. Efforts have kept Everglades National Park largely free of *Melaleuca*. During the past five years, an Everglades crew has removed *Melaleuca* to the east within 8 km outside the eastern park boundary. Big Cypress Na-

[8]A. Jones, 1992, personal communication.
[9]R. Curry, 1992, personal communication. Biscayne National Park, Homestead, FL.

tional Preserve also has an aggressive program of *Melaleuca* control. Their strategy involves timing of burn treatments during vulnerable points in the species' life cycle and integrating burning with appropriate herbicide treatments (Myers and Belles 1992).

Hurricane Andrew may exacerbate the *Melaleuca* problem by dispersing propagules (small branches with seed capsules) to new areas. Hurricane winds along the north edge of the eye would have tended to disperse *Melaleuca* propagules into the park from the east. Successful germination and survival depend on soil moisture conditions.

Brazilian peppertree *Schinus terebinthifolius* (Anacardiaceae) is perhaps the most serious alien plant threat to native vegetation within the Everglades. It can tolerate a wide range of hydroperiods (0–6 months) and is somewhat salt tolerant. Beginning in the late 1970s, it has extensively invaded hammocks, beaches, and higher (less wet and less saline) areas within the mangrove zone, and as of 1987 was found to be invading within a zone covering 39,000 ha or approximately 10% of the land area of the park.[10] *Schinus* has been increasing geometrically in this zone. It now occupies most areas of the Everglades where it can grow. Although the life history of *Schinus* is not well adapted to hurricane dispersal, widespread hurricane disturbance may favor this species in the mangrove zone (Smith et al. page 256 this issue).

The major area of Australian pine (*Casuarina* spp.) within Everglades National Park (the southeastern corner) was outside the main path of Andrew. However, a high density of *Casuarina glauca* also occurs within the East Everglades in the northeastern corner of the park, which was within the hurricane's path. Many of these individuals were windthrown, but we expect abundant resprouting. After Hurricane Donna in 1960 (see page 261), seeds of *Casuarina litorea* were dispersed to beaches of the Gulf Coast, requiring an active removal program in the 1970s to mitigate the impact of this species on turtle nesting and beach erosion. Although the storm surge from Andrew was much less on the Gulf Coast than from Donna, large-scale dispersal of *Casuarina* by the recent storm is a possibility. The storm surge that occurred on the Biscayne National Park islands may also result in the need for *Casuarina* control on Gulf Coast beaches in coming years.

Colubrina asiatica has been an aggressive invader in coastal hammocks of the Everglades and Key Biscayne since the mid-1970s. It has been increasing gradually and could respond rapidly to open canopy and

Hurricane Andrew may have significantly facilitated spread of the Australian paperbark tree, *Melaleuca quinquenervia*, in South Florida wetlands. The dense paperbark stand shown here illustrates the end point in conversion of sedge- and grass-dominated marsh to *Melaleuca* forest. Photo: Martin Fleming.

[10]M. Rose, 1992, personal communication. South Florida Water Management District, West Palm Beach.

smother surrounding vegetation. Other invasive species that are candidates for explosive spread after Hurricane Andrew are *Scaevola taccada* (a Pacific coastal species), *Oeceoclades maculata* (a ground orchid invasive in hammocks), and tree species such as *Albizia lebbeck*, *Bischofia javanica*, and *Schefflera actinophylla*.

Potential consequences of Hurricane Andrew

The entire vegetation mosaic of southern Florida has been in flux throughout its development—shaped by fires, floods, freezes, hurricanes, and sea-level fluctuations (Craighead 1971, Olmsted and Loope 1984, Robertson 1955). We should view the long-term biological consequences of a severe hurricane from such a perspective. Therefore, effects might be minimal and would be no more negative than positive from the standpoint of biological conservation. Such a view should be tempered, however, by concerns for rare species and for invasive exotic species.

Periodic loss of rare species is clearly a natural consequence of a dramatically fluctuating environment. Storms have brought new West Indian migrant species to South Florida, and storms have eliminated species for millenia. The new factor is that humans have increased the potential for chance extinctions of rare taxa by reducing habitats and population numbers.

Other than direct obliteration of vegetation by human development, we expect the spread of introduced plant species to comprise the most dramatic alteration of natural vegetation in South Florida in coming decades. Spread of these invaders was already rapid before Hurricane Andrew. The hurricane may accelerate the process by dispersing propagules and opening forest canopies.

A final cautionary note involves fire; human hydrologic alteration as well as the suppression and ignition of fires influence the fire regimes of South Florida. The potential for destructive fires exists if severe drought coincides with the fuel buildups and open-canopy conditions in hammocks within a few years after the hurricane.

Acknowledgments

We must thank the people, too many to name, who helped our Upland Resource Assessment Team accomplish its mission. We especially thank those who assisted substantively in providing information for this manuscript. They are T. Armentano, O. L. Bass, H. Belles, R. E. Bennetts, R. Curry, S. Husari, R. Labisky, D. Lentz, A. Pernas, W. B. Robertson, S. Sparks, and M. Yordan.

References cited

Avery, B. N., and L. Loope. 1980. Endemic taxa in the flora of south Florida. South Florida Center Report T-558, Homestead.

Baggett, H. D. 1982. Schaus' swallowtail. Pages 73–74 in R. Franz, ed. *Rare and Endangered Biota of Florida. vol. 6. Invertebrates.* University Presses of Florida, Gainesville.

Craighead, F. C. Sr. 1971. *The Trees of South Florida. vol. 1. The Natural Environments and Their Succesion.* University of Miami Press, Coral Gables, FL.

Craighead, F. C. Sr., and V. C. Gilbert. 1962. The effects of Hurricane Donna on the vegetation of southern Florida. *Quart. J. Fla. Acad. Sci.* 25: 1–28.

Deisler, J. E. 1982. Florida tree snail. Pages 15–18 in R. Franz, ed. *Endangered Biota of Florida. Vol. 6. Invertebrates.* University Presses of Florida, Gainesville.

Duever, M. J., J. E. Carlson, and L. A. Riopelle. 1984. Corkscrew Swamp: a virgin cypress strand. Pages 334–348 in K. C. Ewel and H. T. Odum, eds. *Cypress Swamps.* University Presses of Florida, Gainesville.

Duever, M., and McCollom. 1992. Major structural damage present prior to Hurricane Hugo in old-growth forest trees at Four Holes Swamp, South Carolina. *Bulletin of the Ecological Society of America* 73: 161.

Emmel, T. C. 1992. A field survey of endangered species habitats and tropical hardwood hammocks in South Florida following Hurricane Andrew—August 28–30, 1992. *Florida Naturalist* Fall: 12–13, 15, 21–22.

Everglades National Park. 1991. Fire Management plan and environmental assessment. Homestead, FL.

_____. 1992. Hurricane Andrew fuels and fire behavior assessment. Fire Management Program, Homestead, FL.

Frangi, J. L., and A. E. Lugo. 1991. Hurricane damage to a flood plain forest in the Luquillo Mountains of Puerto Rico. *Biotropica* 23: 324–335.

Deisler, J. E. 1982. Florida tree snail. Pages 15–18 in R. Franz, ed. *Rare and Endangered Biota of Florida. vol. 6. Invertebrates.* University Presses of Florida, Gainesville.

Hofstetter, R. H. 1991. The current status of *Melaleuca quinquenervia* in southern Florida. Pages 159–176. in T. D. Center, R. F. Doren, R. L. Hofstetter, R. L. Myers, and L. D. Whiteaker, eds. *Proceedings of the Symposium on Exotic Plant Pests.* US Department of the Interior, National Park Service, Washington, DC.

Long, R. W. 1974. Origin of the vascular flora of South Florida. Pages 28–36 in P.J. Gleason, ed. *Environments of South Florida: Present and Past.* Miami Geological Society Memoir 2.

Loope, L. L., and G. N. Avery. 1979. A preliminary report on rare plant species in the flora of National Park Service areas of South Florida. South Florida Research Center Report M-548, Homestead, FL.

Myers, R. L., and H. A. Belles. 1992. Life history stages, environmental stresses, and the timing of treatments in the control of *Melaleuca quinquenervia* in south Florida. *Bulletin of the Ecological Society of America* 73: 282–283.

Olmsted, I. C., and L. L. Loope. 1984. Plant communities of Everglades National Park. Pages 167–184 in P. J. Gleason, ed. *Environments of South Florida: Present and Past.* Geological Society of Miami Memoir.

Olmsted, I. C., W. B. Robertson Jr., J. Johnson, and O. L. Bass Jr. 1983. The vegetation of Long Pine Key, Everglades National Park. Report SFRC-83/05. South Florida Research Center, Everglades National Park, Homestead, FL.

Patterson, G. A., and W. B. Robertson Jr. 1981. Distribution and habitat of the red-cockaded Woodpecker in Big Cypress National Preserve. South Florida Research Center Report T-613, Homestead, FL.

Robertson, W. B. Jr. 1953. A survey of the effects of fire in Everglades National Park. Everglades National Park, Homestead, FL.

_____. 1955. An analysis of the breeding bird populations of tropical Florida in relation to the vegetation. Doctoral thesis, University of Illinois, Urbana.

Smith, T. J. III, M. B. Robblee, H. Wanless, and T. W. Doyle. 1994. Mangroves, hurricanes, and lightning strikes. *BioScience* 43: 256–262.

Snyder, J. R., A. Herndon, and W. B. Robertson Jr. 1990. South Florida rockland. Pages 230–277 in R. L. Myers and J. J. Ewel, eds. *Ecosystems of Florida.* University of Central Florida Press, Orlando.

Tomlinson, P. B. 1980. *The Biology of Trees Native to Tropical Florida.* Harvard University Press, Cambridge, MA.

Walker, L. R. 1991. Tree damage and recovery from Hurricane Hugo in Luquillo Experimental Forest, Puerto Rico. *Biotropica* 23: 379–385.

Walters, J. R. 1991. Application of ecological principles to the management of endangered species: the case of the red-cockaded woodpecker. *Annu. Rev. Ecol. Syst.* 22: 505–523.

Whigham, D. F., I. Olmsted, E. C. Cano, and M. E. Harmon. 1991. The impact of Hurricane Gilbert on trees, litterfall, and woody debris in a dry tropical forest in the northeastern Yucatan Peninsula. *Biotropica* 23(4a): 434–441.

Yih, K., D. H. Boucher, J. H. Vandermeer, and N. Zamora. 1991. Recovery of the rain forest of southeastern Nicaragua after destruction by Hurricane Joan. *Biotropica* 23: 106–113.